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Plant trait variation along environmental indicators to infer global change impacts☆

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ABSTRACT

One of the key principles for modeling future impacts of anthropogenic and climate changes on vegetation is to identify clear patterns and trends between plant functional traits and ecological drivers. The global spectrum of plant form and function outlines the major axes of variation and coordination among plant traits. We hypothesized that inter-specific plant trait variation at the regional scale should match axes of plant adaptation highlighted by the global spectrum, and that plant trait–environmental associations should be evident over ranges of environmental indicators corresponding to key drivers of future climate and land use changes in Southern Europe. To test our hypotheses, we analyzed a sample of 1095 plant species from Northern Italy, also characteristic of Southern European vegetation. We analyzed trends for four plant traits (canopy height, leaf area, specific leaf area, leaf nitrogen content) along meso- (temperature, continentality) and micro-climatic (light) ranges, as well as along soil ranges (moisture, reaction and nutrient content), by means of Landolt's environmental indicators. At the regional scale, the inter-specific variation of mean plant traits over ranges of environmental indicators confirmed the main axes of plant adaptation emphasized by the plant global spectrum. Leaf area and specific leaf area showed the largest sensitivity over ranges of all environmental indicators, while canopy heights were the most responsive to temperature values. Temperature, light conditions and nutrients were associated with clear effects on plant traits, underlining that responses to changes in land use and increased soil nutrient loading (sudden and abrupt changes) could trigger and strengthen responses to climate alteration (gradual changes). Scenarios for the next few decades in Southern Europe indicate increased temperature, nutrient availability and forest coverage that, according to our findings, will favor more 'acquisitive and fast growing' plants, also represented by subtropical invasive species.

1. Introduction

In the Anthropocene epoch, human activities have changed the global climate, land cover and biodiversity at unprecedented rates, exacerbating negative effects on plant diversity (Parmesan, 2006; Walther et al., 2002). Worldwide impacts of global change are a cause of concern for future scenarios in plant diversity alteration (Parmesan and Hanley, 2015), and its cascade effects on ecosystem functioning and the provision of services (Chapin et al., 2000; Naeem et al., 2009). In Southern Europe, in future decades a rise in temperatures and eutrophication are expected due to an increase in nitrogen deposition, while the concomitant increase in forested areas will lead to an overall decline in light availability (EEA, 2017a, 2017b; Kovats et al., 2014; Leip et al., 2015; Rounsevell et al., 2006; Tilman et al., 2001).

Responses of plant communities to climate change depend strongly on the functional ecology of species (Suding et al., 2008), an aspect of their biology that has been increasingly investigated in recent decades, thanks to an increasing number of studies on Plant Traits (PTs) (Garnier et al., 2017). PTs are among the best proxies used to observe plant responses to changes in environmental conditions (Lamarque et al., 2014; Vandewalle et al., 2010). They integrate the ecological and evolutionary history of a species, thereby reflecting trade-offs among different functions within a single plant and determining species ecological roles in the environment (Violle et al., 2007). PTs influence plant fitness via their effects on resource acquisition, growth, reproduction and survival (Dıaz and Cabido, 2001). Indeed, they quantify the functional dimensions of plants and are fundamental to detect their ecological strategies (Grime and Pierce, 2012; Pierce et al., 2017).

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Extensive studies focused on the plant economics spectrum found evidence that support the 'traits manifesto' (Reich, 2014). Globally the two main axes of functional variation in vascular plant traits (Díaz et al., 2016) are those related to the size of organs and whole plant, and those associated with leaves, the leaf economics spectrum (Wright et al., 2004). The first dimension denotes the ability of plants to make use of light resources, disperse diaspores, and their colonization ability in space and time. It runs from short and small-leaved species tending to have small diaspores to tall and broad-leaved species tending to have large diaspores, broadly reflecting the r (colonization) versus K (exploitation) continuum. The second dimension indicates how plants acquire and use resources. It represents the variation from large leaves with high specific leaf area and leaf nitrogen content, to small leaves with low specific leaf area and leaf nitrogen content, which is a trade-off among 'fast and acquisitive' to 'slow and conservative' growth.

PTs have been shown to vary along ecological gradients for at least some sites and combinations of species (e.g., Ackerly et al., 2002; Herben et al., 2018; Shipley et al., 2017). Nevertheless, there is still no clear consensus about which PTs best predict climate change responses (Parmesan and Hanley, 2015). The links with a single ecological driver have only rarely been systematically evaluated, since it requires a large sampling effort (Rosbakh et al., 2015), although it is a necessary step toward an accurate mapping of current or future spatial distribution of PTs (Butler et al., 2017; van Bodegom et al., 2014; Wright et al., 2017). Selection pressures of defined ecological drivers should generate predictable variation of PTs following the main axes of adaptation within the plant economics spectrum, at least at the inter-specific level (Vellend et al., 2014), providing useful opportunities to explore the ability of plants to respond to global changes.

In this context, Environmental Indicators (EIs) (Ellenberg et al., 1992; Landolt et al., 2010) could be suitable, since they are scores for each single species representing their average position within the range of key ecological drivers. They have been criticized since they are derived from the personal observations of authors and do not rely on objective measurements (Shipley et al., 2017). However, they have a long history of validation (e.g., Klaus et al., 2012; Scherrer and Körner, 2011; Thompson et al., 1993; Wamelink et al., 1998), so they may provide an early warning signal of changes in the environment. For this reason, they have been widely applied in studies of vegetation ecology as well as studies concerning global changes (Diekmann, 2003; Scherrer and Körner, 2011). In the context of the plant's competitive situation, PTs should vary accordingly to EIs, depending on the environmental filters, since EIs represent coordinates of plants' niche in natural communities as defined by their physiological growth limits (Landolt et al., 2010). Hence, insights from the analysis of mean values of PTs along EIs ranges could reconcile two main fields of ecology. This could provide a deeper understanding of plant functional responses to future climate and land use changes, especially considering trends in PTs and their responses at the extremes of EI ranges.

In this study, we evaluated the extent of inter-specific variation of key PTs of the plant global spectrum (Díaz et al., 2016) along a range of ecological drivers. To this end, we studied a large sample of vascular plants form Southern Europe, and estimated ecological drivers using the EI scores of the study species. Firstly, we hypothesized that inter-specific variation of PTs at the regional scale should match the major axes of plant adaptation highlighted by the plant global spectrum (Díaz et al., 2016). Secondly, variation over ranges of EIs should correspond to PT variation along gradients of key ecological drivers of global changes (temperature, rainfall, light and N availability, soil reaction and moisture).

2. Methods

2.1. Plant traits (PTs)

In accordance with the plant global spectrum (Díaz et al., 2016), we selected two "size" traits (Canopy Height and Leaf Area, respectively CANH and LA), and two traits linked to the "leaf economics spectrum" (Specific Leaf Area and Leaf Nitrogen Content per leaf dry mass, respectively SLA and LNC). PT data were selected from Authors datasets available in TRY (Kattge et al., 2011; https://www.try-db.org/: see datasets n. 227, 228, 229, 371, 372 and related references), augmented with some previously unpublished data from our own database.

For each species, within the same population we sampled from 5 to 15 fully expanded leaves selected randomly from the outer canopy of different individual adult plants growing under optimal conditions, following a standardized methodological protocol (Perez-Harguindeguy et al., 2016). We measured CANH as the maximum vegetative height: distance between the ground and the highest vegetative leaves of the plant (i.e. excluding inflorescences; Perez-Harguindeguy et al., 2016). For this measure, we selected the tallest individual of each species among those identified for leaf sampling. Plants were measured in their normal state, i.e. without stretching them. CANH was quantified in situ, while all the other PTs were determined from analysis of material collected in the field and analysed in the laboratory. For LNC we processed three replicates (each from a single individual shoot) from dry leaf material with a CHNS-analyzer (FlashEA 1112 series ThermoScientific). More detailed methodological protocol concerning collection of leaf material and sample processing procedures are reported in Cerabolini et al. (2010).

Sampling sites (n = 154) are widespread over an area of approximately 89,000 km^2, covering 22 provinces of Northern Italy. Almost all records of our dataset (96%) are representative of vegetation types of Alpine (Southern Alps) and Continental (Po Plain) biogeographic zones (ETC/BD, 2006) (Fig. 1). Except for some samples from the Mediterranean biogeographic region, the climate ranges from continental to oceanic regimes (Pesaresi et al., 2014), although the complex morphology of the study area results in considerable variability of mesoclimates, from warm climates close to the main lakes, to middle-European of lowland areas and to cold Alpine regimes of high elevation. Substrates vary from silicatic or carbonatic rocks to sedimentary deposits of various sources, with additional extensive variability at the local scale.

2.2. Environmental indicators (EIs)

EIs for the vascular plants of Central Europe (see Ellenberg et al., 1992) have also been determined for many floras of adjacent regions. Those published for the Swiss flora have a long tradition culminating with the 2010 edition of the Flora Indicativa (Landolt et al., 2010), that we considered the most suitable to describe species distribution along ranges of ecological drivers in our study area, since it neighbours Switzerland (Fig. 1).

For each species, we considered two meso-climatic (temperature, T; continentality, K), one micro-climatic (light, L) and three soil indicators (moisture, F; reaction, R; nutrients N), allocating them to indicators' classes as reported in Flora Indicativa (Landolt et al., 2010). T characterises the average air temperature during the growth period of a plant, which largely corresponds with the average elevational distribution of species. It ranges from alpine and nival (1) to very warm colline (5). K indicates whether the air is humid and the daily and annual variation of temperature occur within small ranges (small values), or the air is dry and there is a large variation in temperature (high values). It ranges from oceanic (1) to continental (5). L specifies the average light quantity received in the respective habitats. It ranges from deep shade (1) to full light (5). Concerning soil indicators: F is the average soil moisture during the growth period; it ranges from very dry (1) to flooded (5); R is the content of free H-ions in the soils, it ranges from extremely acid (1) to alkaline (5); N is the nutrient content in the soil, referring mostly to nitrogen but also to phosphorus, and spreads from very infertile (1) to very fertile (5).

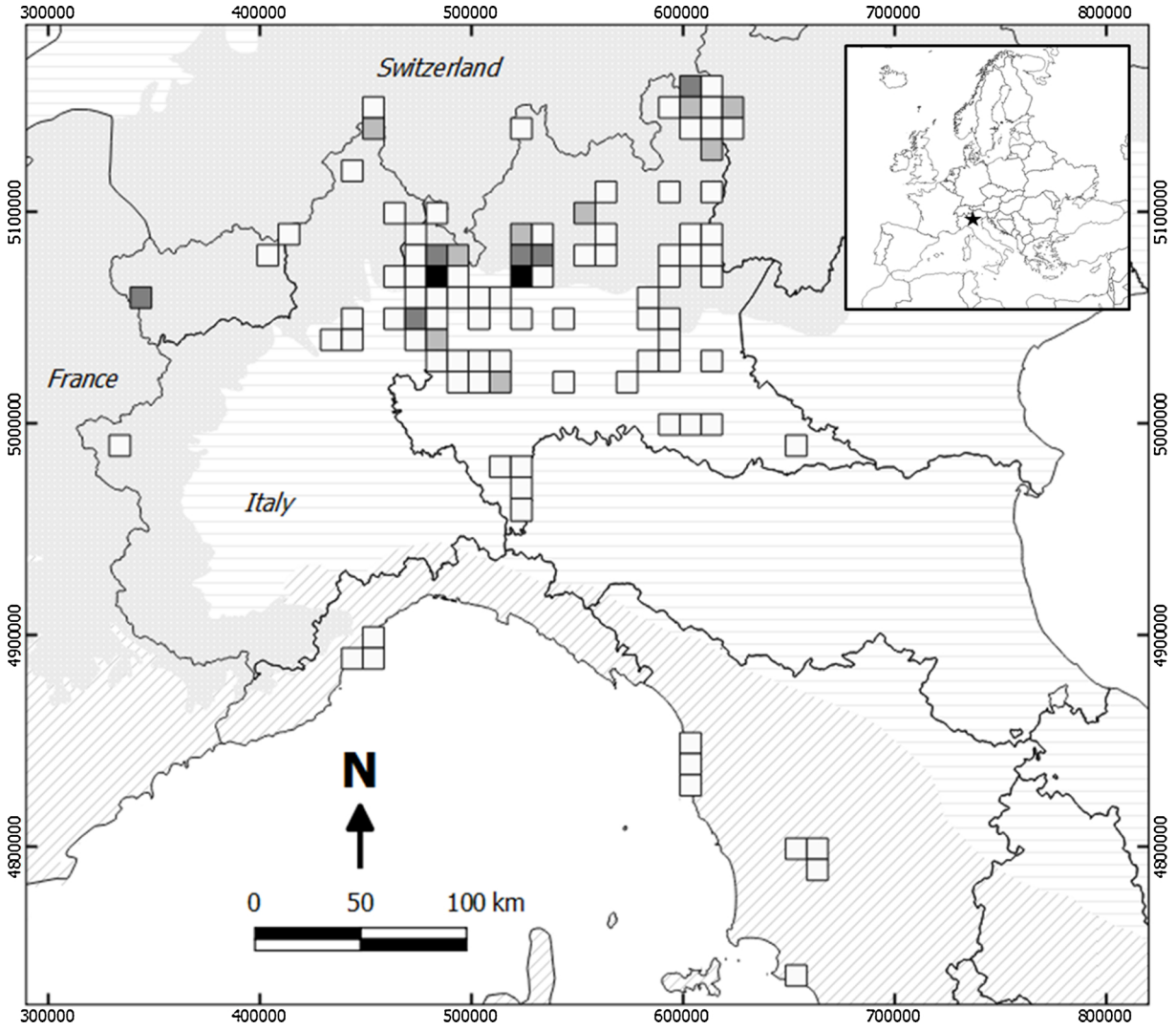

Fig. 1. Map of the spatial distribution of the analysed dataset (reference system WGS84/UTM 32 N). The 10 km × 10 km grid has been categorized using the sum of all records contained in each pixel: 1–15 (white), 16–30 (light grey), 31–50 (dark grey), and 51–150 (black). The black line indicates the administrative borders, i.e. borders of France and Switzerland, and the administrative regions of Italy. Biogeographic regions (ETC/BD, 2006) are indicated: Alpine = dotted grey; Continental = strikethrough horizontal grey, Mediterranean = strikethrough diagonal grey. The black star in the inset map indicates the location of the study area.

2.3. Data analysis

We selected 1095 species from 50 families (Peruzzi, 2010), excluding species of underrepresented families in the overall dataset (i.e. with less than five species); thus the dataset submitted to analysis included 108 trees, 76 shrubs, 209 graminoids and 702 forbs (Appendix A).

LNC analysis were performed on a smaller dataset, due to the lack of available data (838 taxa analyzed), while hydrophytes were excluded from CANH analysis (1057 taxa analyzed). We also excluded species indifferent to a single EI, marked as “x” in Landolt et al. (2010), from analysis concerning that EI (Appendix B). However, the proportion of “x” species was always small, ranging from 0% (L and N) to 1.2% (LNC vs T).

According to Landolt et al. (2010), each EI has its own scale of indicator values, mainly a unit increment ranging from 1 to 5. In T and F the 1 to 5 range is split into 0.5 unit increments, resulting in 9 classes. To be able to compare the results among EIs, we assigned species with “intermediate” values to the next unit class toward the extremes of the range (i.e. 1.5 to 1, 2.5 to 2, 3.5 to 4, and 4.5 to 5).

Data were first normalized by logarithmic (LA, CANH and SLA) or square root (LNC) transformation, and normality checked according to the Shapiro Wilkman test. We compared differences in PTs among the five classes of each EI by means of analysis of variance (ANOVA). We used a linear mixed-effects model, considering the family as a random effect to exclude influences of phylogenetic correlation. For each combination of PTs vs EIs, we tested the effect of family via ANOVA, comparing the results of the linear mixed-effects model with those of a general linear model, considering only the classes of EIs as factors. The addition of family on the models was always highly significant ($p < 0.01$). Post-hoc comparisons on the results of linear mixed-effects models were then calculated by Tukey's test. For PTs showing statistically significant differences following post-hoc comparison, we estimated the regression trend for the means of PTs along the classes of EIs using linear or non-linear regression (quadratic) models. We selected the most significant regression trend comparing the two models through ANOVA. We then compared the effect sizes of EIs and their interactions on each PT through a multifactorial ANOVA with interactions, using eta squared (η^2) to quantify the effect sizes (Levine and Hullett, 2002). All the statistical analyses were computed with R software (R Core Team, 2017).

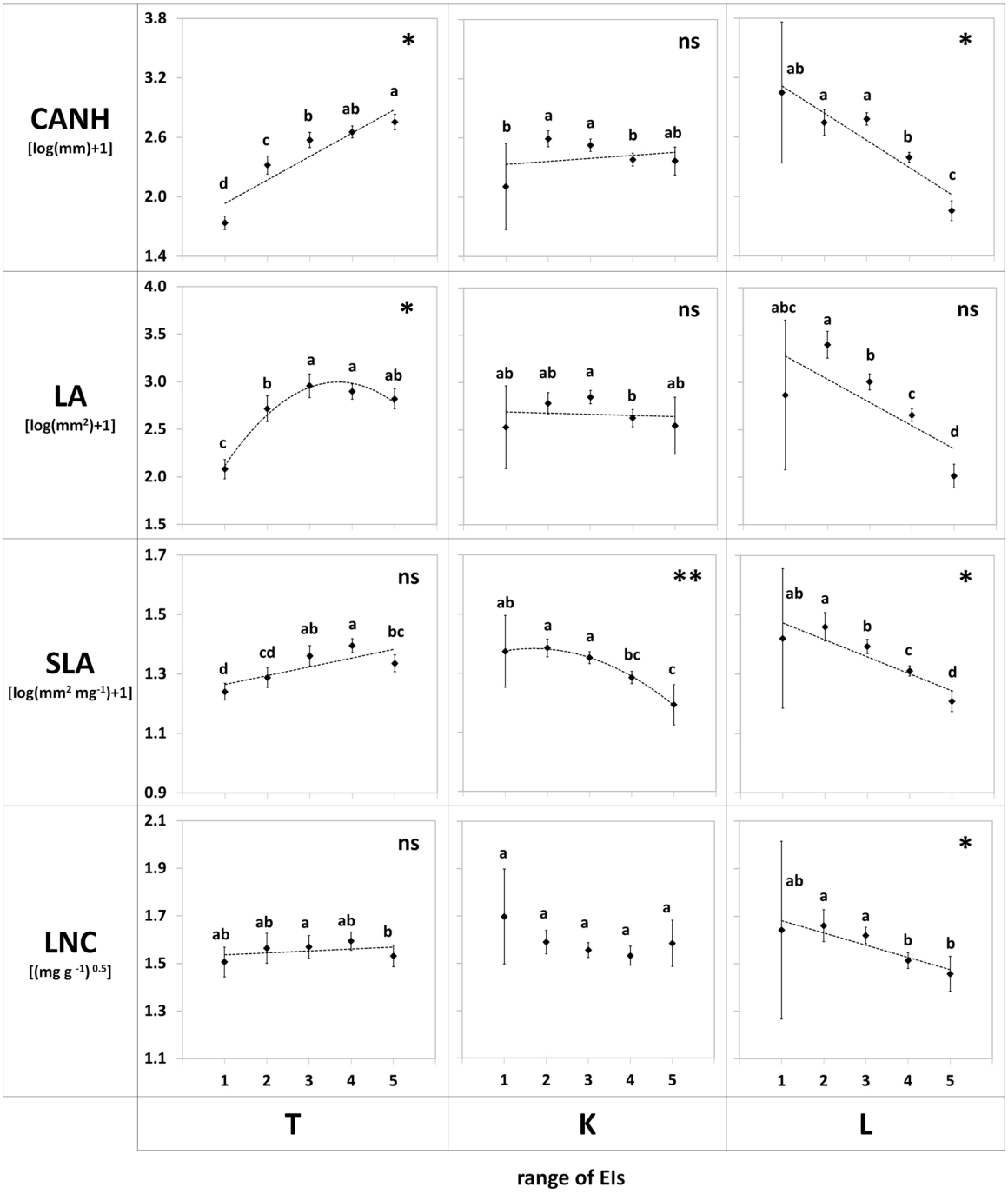

Fig. 2. Mean (± 1.96*SE) of Plant Traits–PTs (CANH = Canopy Height, LA = Leaf Area, SLA = Specific Leaf Area, LNC = Leaf Nitrogen Content) vs climatic Environmental Indicator classes–EIs (T = Temperature, K = Continentality, L = Light) according to Landolt et al. (2010). Lower-case letters indicate the results from Tukey post-hoc comparison following ANOVA. Regression trends between PTs and EIs are plotted only when ANOVA with Tukey post-hoc comparison was statistically significant: (ns) p-value > 0.05; (*) p-value ≤ 0.05; (**); p-value ≤ 0.01.

3. Results

3.1. Canopy height (CANH)

With regard to meso- and micro-climatic EIs (Fig. 2), CANH showed highly significant differences in terms of T ($F_{4,995}$ = 111.7, p < 0.001) and L ($F_{4,1006}$ = 65.7, p < 0.001) ranges, while differences were less distinct for K ($F_{4,1003}$ = 4.8, p < 0.001). Mean canopy heights were significantly shorter in species of the lowest temperature regimes (T = 1) and increased progressively reaching the maximum in species of higher temperature regimes (T = 4 and T = 5). Mean canopies showed an overall significant linear decrease along the L range: they were higher in moderate shade classes (L = 2 and L = 3) and lower in well-lit (L = 4) and mostly in full light (L = 5) classes. On the other hand, deep shade species displayed a slightly opposing trend, but represented a small proportion of the dataset (about 0.2%) (Appendix B), and this may have affected the outcome.

Among soil EIs (Fig. 3), CANH exhibited significant differences only over the R ($F_{4,995}$ = 24.2, p < 0.001) and the N ($F_{4,1006}$ = 46.3, p < 0.001) ranges, since we found weak significant differences among F classes ($F_{4,1001}$ = 2.4, p = 0.05) with no significant post-hoc comparisons (p > 0.05). However, while the CANH differences over R

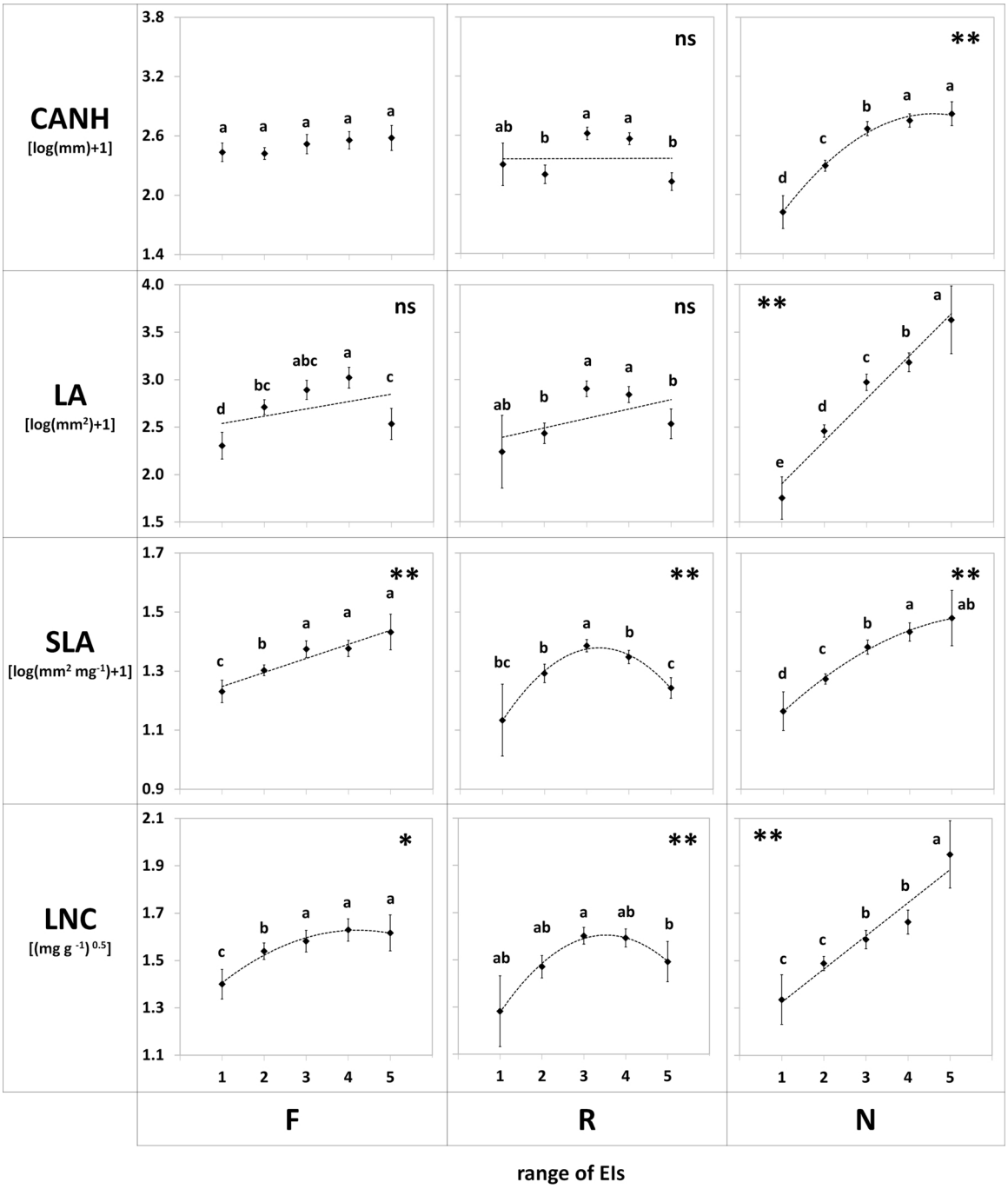

Fig. 3. Mean (± 1.96*SE) of Plant Traits–PTs (CANH = Canopy Height, LA = Leaf Area, SLA = Specific Leaf Area, LNC = Leaf Nitrogen Content) vs soil conditions Environmental Indicator classes–EIs (F = Moisture, R = Reaction, N = Nutrients) according to Landolt et al. (2010). Lower-case letters indicate the results from Tukey post-hoc comparison following ANOVA. Regression trends between PTs and EIs are plotted only when ANOVA with Tukey post-hoc comparison was statistically significant: (ns) p-value > 0.05; (*) p-value ≤ 0.05; (**); p-value ≤ 0.01.

classes did not show a clear trend, over the N range they showed a statistically significant non-linear increase, consisting of a saturation in the two higher N classes of fertile and over-rich soils (N = 4 and N = 5). The lowest mean canopy heights were those of very infertile soils (N = 1).

3.2. Leaf area (LA)

Mean LA showed significant differences over all the climatic EI (Fig. 2) ranges: T ($F_{4,1030}$ = 36.8, p < 0.001), K ($F_{4,1038}$ = 2.9, p = 0.02) and L ($F_{4,1041}$ = 54.0, p < 0.001). Leaves were on average significantly smaller in species of the lowest temperature regimes (T = 1) and progressively larger in warmer classes, showing a slight decrease in the warmest one (T = 5). Mean LA was also significantly higher in species of intermediate moisture climates (K = 3) but a clear pattern of leaves size was not detectable towards the extremes of the K range. Concerning light availability, along L range mean LA progressively decreased moving from shade to full light conditions (i.e. from L = 2 to L = 5), although the trend was not significant. Outcomes may be affected by the shortage of deep shade species in the dataset, as mentioned above.

LA displayed highly significant differences over all the soil EI ranges

(Fig. 3): F ($F_{4,1036}$ = 16.2, p < 0.001), R ($F_{4,1030}$ = 12.5, p < 0.001) and N ($F_{4,1041}$ = 67.0, p < 0.001), although the evident non-linear layouts highlighted along F and R ranges by post-hoc comparisons were not supported by significant regressions. Mean LA was smaller in species growing in dry and very dry soils (F = 1) and in wet and flooded soils (F = 5), if compared to moist soils species (F = 4). At the same time, mean LA was significantly smaller in species growing in acid (R = 2) and alkaline soils (R = 5) but larger for species from soils at intermediate reaction (R = 3 and R = 4). A clear progressive increase of mean LA was evident throughout the range from very infertile (N = 1) to very fertile and over-rich soils (N = 5).

3.3. Specific leaf area (SLA)

Mean SLA showed highly significant differences along all the meso and micro-climatic EI ranges (Fig. 2): T ($F_{4,1030}$ = 13.2, p < 0.001), K ($F_{4,1038}$ = 14.8, p < 0.001) and L ($F_{4,1041}$ = 37.2, p < 0.001). Leaves were on average tougher (low values of SLA) in species from low temperature regimes of high elevation (T = 1 and T = 2) compared to those from warmer climates of the montane and colline belts (T = 3 and T = 4). Species proper of warmest climates (T = 5) showed a slight decrease of mean SLA, and they were significantly different only from those of the colline belt (T = 4). Nevertheless, the trend of mean SLA over the T range was not significant. Mean SLA values were significantly higher in species from climates under oceanic influence (from K = 1 to K = 3) and lower in those linked to continental regimes (K = 5), as underlined by the highly significant non-linear trend. Mean SLA values decreased linearly as light availability increased, being higher in species growing in shade (L = 2) and lower in those linked to full light sites (L = 5). The slight decrease of mean SLA in deep shade species (L = 1) can likely be due to the shortage of deep shade species in the dataset, as mentioned above.

Mean SLA also displayed significant differences throughout all the soil EI ranges (Fig. 3): F ($F_{4,1036}$ = 26.0, p < 0.001), R ($F_{4,1030}$ = 12.3, p < 0.001) and N ($F_{4,1041)}$ = 27.4, p < 0.001). Species linked to very dry soils (F = 1) showed the lowest value of mean SLA, which increased linearly in species growing in moderate dry soils (F = 2) and again in those from moderately moist to flooded soils classes (F = 3, F = 4, F = 5), but with no further differences. Along the R range, the highest value of mean SLA occurred in species of the intermediate class representing almost neutral soils (R = 3), while comparable low mean SLA values belonged to species of extremely acid (R = 1) or alkaline soil (R = 5) classes. Mean SLA values clearly increased alongside nutrient availability, until an asymptotic saturation appeared from medium fertile to over-rich soils (N = 3, N = 4, N = 5).

3.4. Leaf nitrogen content (LNC)

Among the climatic EI ranges (Fig. 2), mean LNC showed significant differences over T ($F_{4,774}$ = 2.9, p = 0.02) or L ($F_{4,784}$ = 7.9, p < 0.001) classes, while no significant differences were found over K classes ($F_{4,782}$ = 1.9, p = 0.11). However, mean LNC values did not display a significant trend along T range and the post-hoc comparisons showed significant differences only between species of two classes (T = 3 vs T = 5). On average, mean LNC values were significantly higher in species linked to moderate shade (L = 2, L = 3) compared to those assigned to well-lit and full light classes (L = 4, L = 5), resulting in a linear decreasing trend of mean LNC as light availability rose. Species of deep shade did not show any differences.

Conversely, mean LNC displayed significant differences along all the soil EI ranges (Fig. 3): F ($F_{4,781}$ = 14.8, p < 0.001), R ($F_{4,777}$ = 4.1, p < 0.003) and N ($F_{4,784}$ = 14.1, p < 0.001). It was significantly lower in species linked to dry soils (F = 1), then increased until saturation in species linked to classes of F indicating moderate moist to flooded soils (from F = 3 to F = 5). Along the R range, a non-linear trend was readily detectable, although in the post-hoc comparisons significant differences emerged only between species from neutral soils (R = 3) and those linked to alkaline soils (R = 5), the first ones showing a higher mean LNC value. Ultimately, mean LNC values revealed a significant marked linear increase along N range, with lower values belonging to species of very infertile and infertile soil classes (N = 1, N = 2) and higher values in species linked to very fertile and over-rich soils (N = 5).

4. Discussion

Our analyses, based on a large dataset, broadly confirmed at the regional scale of Southern Europe the main axes of adaptation of vascular plants determined by the global spectrum of plant form and function (Díaz et al., 2016). Whole plant size, represented by CANH, and organ size, represented by LA, showed similar responses and consistent trends throughout all the EI ranges, although with slightly different levels of significance. Similarly, but more evidently, SLA and LNC varied over EI ranges in agreement with the leaf economics spectrum (Wright et al., 2004).

At a broad scale, we observed a general response of PTs to environmental associations depicted by Landolt's EIs. Among these, we found subtle patterns of PT variation associated with continentality (K) while the most remarkable patterns concerned soil nutrient content (N).

In a very schematic way we can state that, 'size' PTs (CANH and LA) were influenced more by meso- and micro-climatic EIs (T and L), while PTs representing the leaf economics spectrum (SLA and LNC) exhibited evident responses to soil EIs (F, R and N). However, the occurrence of synergic effects due to shifts in environmental drivers should always be taken into account, although our analysis concerning the interactions between couples of EIs mainly exhibited no significance or small effect sizes (Table 1). On the other hand we must consider that environmental drivers will likely act in an asynchronous way, since climate warming may occur more gradually compared to more abrupt changes in land use, especially with regard to local soil nutrients loadings (eutrophication), so that the former will act on vegetation assets modified by the latter.

Table 1
Effect sizes (eta squared, η^2) and significance (p-value) of each environmental indicator, and their interactions, on plant traits (CANH = Canopy Height, LA = Leaf Area, SLA = Specific Leaf Area, LNC = Leaf Nitrogen Content) as inferred by multifactorial ANOVA with interactions.

	CANH		LA		SLA		LNC	
	η^2	p-value	η^2	p-value	η^2	p-value	η^2	p-value
T	**0.269**	***	**0.124**	***	**0.052**	***	0.009	ns
K	**0.016**	***	**0.016**	***	**0.028**	***	0.003	ns
L	**0.065**	***	**0.090**	***	**0.043**	***	**0.037**	***
F	**0.012**	***	**0.052**	***	**0.027**	***	**0.033**	***
R	0.003	ns	**0.017**	***	**0.021**	***	**0.029**	***
N	**0.015**	***	**0.064**	***	**0.016**	***	**0.041**	***
T*K	**0.019**	**	0.009	ns	0.012	ns	**0.026**	*
T*L	**0.012**	*	0.008	ns	**0.025**	**	**0.026**	*
T*F	0.012	ns	0.007	ns	0.013	ns	0.02	ns
T*R	0.011	ns	0.015	ns	0.013	ns	0.014	ns
T*N	0.008	ns	0.012	ns	0.012	ns	0.014	ns
K*L	**0.014**	*	0.011	ns	0.016	ns	0.016	ns
K*F	0.007	ns	**0.021**	**	0.017	ns	0.014	ns
K*R	0.006	ns	0.010	ns	0.006	ns	0.014	ns
K*N	0.004	ns	**0.013**	*	0.009	ns	0.008	ns
L*F	0.011	ns	0.009	ns	**0.018**	*	**0.028**	*
L*R	0.012	ns	0.002	ns	0.015	ns	0.017	ns
L*N	0.005	ns	0.005	ns	0.004	ns	0.006	ns
F*R	**0.015**	*	0.015	ns	0.011	ns	0.013	ns
F*N	0.014	ns	0.009	ns	0.014	ns	0.011	ns
R*N	0.005	ns	0.006	ns	0.005	ns	0.006	ns

Legend: (ns) p > 0.05; (*) p ≤ 0.05; (**) p ≤ 0.01; (***) p ≤ 0.001. Emboldened factors are those statistically significant.

We are well aware of the critical points of our broad approach that need to be followed up by more detailed and deeper analyses to validate and to fine-tune our outcomes. For example, differential responses over EI ranges may be expected by dividing the traits dataset used here among growth forms (Shipley et al., 2017) or plant strategies (Pierce et al., 2017), or further considering intra-specific traits variation along better defined gradients (Vellend et al., 2014) to gain insights with regard to species' chances of acclimatization when faced with changing ecological conditions.

4.1. Climate indicators

Our data showed the largest effect size scores in relation to the T range for CANH and LA (Table 1), evidence that agrees with the fact that temperature rise will undoubtedly be the major environmental driver of climate change determining future vegetation distributions. From low to high temperature regimes we found, in accordance with previous studies, groups of species with higher mean canopy height (Sandel et al., 2016; Tardella et al., 2016) and bigger mean size of leaves (Hodgson et al., 2011; Scoffoni et al., 2011; Wright et al., 2017). Temperature regimes had much less effect on traits linked to the leaf economics spectrum, even though we recorded a mean SLA increase from low to high T classes: i.e. passing from 'slow and conservative' to 'fast and acquisitive' leaves (Borgy et al., 2017; Fontana et al., 2017; Rosbakh et al., 2015; Sandel et al., 2016; Wright et al., 2004).

We can therefore assume that warmer climate expected in Southern Europe in future decades (EEA, 2017a; Kovats et al., 2014) will facilitate large-leaved species with taller canopies, and that high elevation vegetation of the Southern Alps will also be affected, as recent findings across the tundra biome have highlighted (Bjorkman et al., 2018). Despite this, at the warmest extreme of the T range, LA, SLA and LNC showed a moderate decrease that fits well with the "laurophyllisation" phenomenon of lower vegetation belts in Southern Switzerland (Walther et al., 2002), although leaf life span was not included in our dataset.

Over the continentality range mean values of traits were the least responsive, probably because of the small amplitude of this range in Switzerland, obscured by the attribution of Mediterranean species to the medium class instead of to the driest one (Landolt et al., 2010). Although an increase of plant height together with precipitation was found for grasslands (Sandel et al., 2016), species in our dataset showed higher mean values in intermediate classes, as observed by Fontana et al. (2017). Our outcomes also cannot corroborate the evidence that broad-leaved species are associated with wetter climates (e.g. Hodgson et al., 2011; Scoffoni et al., 2011; Wright et al., 2017).

Continentality range was associated with a significant decrease of mean SLA values (Table 1) in agreement with previous observations (Hodgson et al., 2011; Rosbakh et al., 2015; Sandel et al., 2016; Shipley et al., 2017; Wright et al., 2004). Accordingly, we can assume that species with more conservative leaves (low SLA) will be favored by the average precipitation decrease predicted in future scenarios (EEA, 2017a; Kovats et al., 2014).

The light availability indicator exhibited significant effects on all PTs (Table 1), which showed a general progressive decrease from shade to full light conditions. Our outcomes are in agreement with competition for light, as shaded habitats are normally associated with 'acquisitive and fast growing' species (Hodgson et al., 2011; Rosbakh et al., 2015; Wright et al., 2004) with taller canopies (Fontana et al., 2017; Tardella et al., 2016). The functional variability of species adapted to deep shade is probably due to the wide array of responses displayed by understory plants (e.g., Valladares et al., 2002). We must also consider that local floras typically include fewer species adapted to deep shade with respect to those living in higher light conditions. For example, considering the whole flora of Switzerland (n = 6472; Landolt et al., 2010), only 0.5% of species are included in the deep shade class. However, distribution of mean LA values along the light availability range did not reveal a significant trend at the inter-specific level considered by our analysis. Leaf area shifts with light availability are probably related to both single species and growth forms (Ackerly et al., 2002). An almost stable pattern of LA along irradiance gradient was observed for herbs and shrubs, while graminoids and trees showed a remarkable decline as irradiance increased (Shipley et al., 2017).

According to the scenario modeled for Southern Europe (Rounsevell et al., 2006), future decades should be characterized by an increase of forested areas at the expense of grasslands, so species that are large, 'acquisitive and fast growing' and/or shade tolerant, will be favored by future land use circumstances.

4.2. Soil indicators

From very dry to moist soils, as expected (Reich, 2014), we observed a gradual shift from 'slow and conservative' to 'fast and acquisitive' species, denoted by the trends of leaf economics PTs (i.e. from low to high SLA and LNC). Similar trends have already been reported in the literature (Fraser et al., 2016; Garnier and Navas, 2012; Herben et al., 2018). However, the increases of mean values of SLA and LNC were evident only in the first part of the range until the mesic condition was reached, and beyond this point the increase of soil moisture did not provide any significant modification of leaf economics PTs. A comparable pattern was also shown by leaf area (Table 1) although this decreased on wet soils, probably due to the contribution of leafless species (see *Cyperaceae* and *Juncaceae*). Small leaves were thus associated with both extremes of soil moisture, according to Shipley et al. (2017). Regardless of local presence of water bodies (rivers, lakes, ponds, mires etc.) soil moisture availability is strongly linked to temperature and precipitation regimes, so that models performed for Southern Europe predict a decrease of soil moisture in future decades (EEA, 2017a; Kovats et al., 2014), which will presumably favour species with relatively conservative strategies.

Over the soil reaction range (R) all the mean values of PTs generally exhibited a convex unimodal relationship, reaching maximum values in the group of species growing in neutral soils. This humped pattern highlights the harsh soil conditions experienced by plants living at both extremes of the range, which are associated with conservative and slow growing species (Garnier et al., 2016), smaller in height and in leaf size (trends of these two latter PTs were not significant). Although responses of plants to soil reaction range were clear, insights concerning future vegetation scenarios driven by this factor are difficult to assess since it presumably will not change rapidly in the near future, being strictly associated with the geological substrate.

Larger plants are expected to be strongly linked to very fertile soils, considering that nitrogen and phosphorus availabilities (to which the N indicator mainly refers; Landolt et al., 2010) are the main limiting factors of plant growth (Güsewell, 2004; Stevens et al., 2018). Hence an increase in soil nutrient availabilities can lead to a parallel increase of values in all the PTs studied here (Ackerly et al., 2002; and references therein). Specifically, from poor to very rich soils plants exhibited consistently taller canopies (Tardella et al., 2016; Herben et al., 2018) and larger leaves (McDonald et al., 2003; Shipley et al., 2017). The two 'size' PTs differed each other only in the highest N class, in which mean values of canopy heights reached saturation.

Conservative strategies (Stress tolerant, *sensu* Grime; see Grime and Pierce, 2012) are linked to nutrient poor soils, while relatively acquisitive strategies (Competitive and Ruderal, *sensu* Grime; see Grime and Pierce, 2012) to nutrient rich soils (Fraser et al., 2016; Garnier and Navas, 2012; Reich, 2014; Wright et al., 2004). This was also clearly shown in our results concerning mean 'leaf economics' plant traits (SLA and LNC), along the entire N range.

Since soil nitrogen and phosphorus loadings in Southern Europe will continue to increase in the future decades (EEA, 2017b; Leip et al., 2015; Tilman et al., 2001), we can expect a rise of larger 'acquisitive and fast growing' species, with an overall enhancement of Competitive

strategies and competition rates in plant communities. This could put a strain on biodiversity at the local scale (Bobbink et al., 2010) according to the rates of eutrophication or nitrogen deposition.

5. Conclusions

Consistent with trait-based niche theory (Reich, 2014), the tendency of species to share PTs is connected to their broad habitat affinities as well as to their ecological niche, which can be described by EIs, at least at a general level. This evidence provides an elementary tool to gain insight into plant functional responses to changes in ecological drivers (Garnier et al., 2016). Among the PTs considered in our work, SLA and LA were responsive to all the ecological ranges identified by Landolt's EIs; hence we suggest that they are very suitable for monitoring of global change impacts. CANH showed the highest sensitivity over the T range, suggesting that species with taller canopies will very likely be favored in warmer scenarios throughout all vegetation types of Southern Europe, until the upper vegetation belts of the Alps (e.g. Bjorkman et al., 2018). Alternatively, land use changes which lead to nutrient increases in soils showed clear-cut effects along both major axes of the global spectrum, so that we can expect larger 'acquisitive and fast growing' species to be favoured, driving a potential increase of total biomass (Gornish and Prather, 2014; Timmermann et al., 2015), consequently changing the competition rates within plant communities. Our results also suggest that future global changes could promote the establishment of further growth forms and functional types, currently only scarcely represented or lacking in Southern European local floras (Walther et al., 2002). Moreover, the globalization of plant species is favouring the introduction of invasive alien species (Ciappetta et al., 2016; Najberek et al., 2017), particularly those native to areas under warmer climates which possess combinations of traits associated with rapid resource acquisition and growth (Gioria and Osborne, 2014; Guo et al., 2018; van Kleunen et al., 2010). This is currently evident in the large number of subtropical invasive species that are already spreading in Southern Europe, including Italy, and threatening local plant diversity (Assini et al., 2010): e.g. *Humulus japonicus* Siebold & Zucc., *Reynoutria japonica* Houtt., *Berberis bealei* Fortune, *Pueraria lobata* (Willd.) Ohwi, *Catalpa ovata* G.Don, *Trachycarpus fortunei* (Hook.) H.Wendl.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.flora.2018.12.004.

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